Observations on Arachnactis albida, M. Sars.

By

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With Plates 3, 4, and 5.

By the courtesy of Mr. T. A. Stephenson, of the University College of Wales, Aberystwyth, I have been entrusted with a portion of the collection of Anthozoa made by the Department of Agriculture and Technical Instruction for Ireland, in the course of marine investigations extending over a number of years. Among these were several gatherings of Arachnactis larvæ, and I have welcomed the opportunity of resuming studies which I began, but never brought to a conclusion, in 1889. At that time little was known of the anatomy and life-history of the Arachnactis larvæ of Cerianthus beyond what was contained in the works of M. Sars (**20**) and A. Agassiz (**1** and **2**), and finding that a species, subsequently named Arachnactis bournei by Fowler (**13**), was a constant element in the plankton collected at Plymouth in the summer months, I selected and preserved for microscopical study as many stages as possible, intending to publish a full account of my investigations of their structure. But hardly was the material for my projected work collected when I was asked to allow the late Prof. E. van Beneden to look at it. I accordingly sent all the specimens of Arachnactis that I possessed to the distinguished Belgian zoologist, without

attaching any conditions to what I regarded as a loan or valuable material. In the absence of such conditions the loan was taken to be a gift. Prof. van Beneden made prompt use of the material that I had provided, and within a year had written the memoir (3) which has to a large extent formed the basis of his own and other subsequent work on the subject. I have no complaint to make against an esteemed and lamented friend. Prof. van Beneden gave me more than my due share of credit in the matter, and doubtless made fuller and better use of the material than I should have done at the time. I only mention the matter now because a survey of the literature, in which my name occurs pretty frequently, suggests that I acted as a mere collector of material and threw away a good opportunity through failure to appreciate the value of what I had preserved. As it happened, a subject which I had hoped to make my own passed into other and very able hands, and the collections that I made were the prelude to the splendid memoir afterwards published by Prof. E. van Beneden (4) on the Anthozoan larvæ of the "National" Expedition. More recently large additions to our knowledge have been made by Fowler, Carlgren, McMurrich and others, and the developmental history of at least two species of Arachnactis has been so fully treated by them that little seems to be left for any subsequent investigator to deal with. But the Irish collections that have come into my hands enable me to fill some gaps in our knowledge of the life-history of one species—A. albida.

The specimens of Arachnactis collected by the Fisheries Branch of the Department of Agriculture for Ireland may be divided into two groups.

I. Those from collections made in the Irish Sea in 1910, from two localities.

1A. May 3rd, 1910 ; 17 miles E. $\frac{1}{2}$ S. of Rockabill. N. lat. 53° 39′ 30″ ; W. long. 5° 32′. Coarse silk and cheesecloth tow-net at 30 fath. This haul gave fifty-four examples of Arachnactis, all at approximately the same stage of development, with 9–11 marginal tentacles. The label bears the

name Arachnactis bournei—a synonym of A. lloydii.
The specimens collected by me at Plymouth in 1889 were
described by van Beneden (**3**) as the "larve de Bourne," but
he did not at first give them a specific name. Subsequently
(**4**) he identified them as the larval forms of Cerianthus
lloydii, but Fowler (**14**) has pointed out that this identifica-
tion is conjectural, and proposed the specific name bournei
for this larva. These examples from the Irish Sea bear a
close resemblance to others of a slightly younger age which
I obtained at Plymouth in 1914.

Iв. Five examples, similar to the above, taken May 12th, 1910,
14 miles S. of Hook Light. N. lat. 51° 54′; W. long. 6° 40′.
Coarse silk and cheesecloth tow-net at 18 fath. Soundings,
38 fath.

I have given in Pl. 3, figs. 1 and 2, outline drawings of one
of these larvæ, to illustrate the marked difference in form
between them and the corresponding stages of Arachnactis
albida, about to be described. The specimen figured has
eleven marginal tentacles, the anterior median tentacle well
developed but shorter than those of the adjacent first couple.
The first, second and third couples of tentacles are fully
formed, the fourth couple much smaller, and the fifth couple
represented by mere nodular swellings. There are only two
couples of labial tentacles, with rudiments of a third couple.
These figures should be compared with Pl. 3, figs. 12 and 13,
representing equivalent growth stages of Arachnactis
albida. In the latter there are three couples of labial
tentacles, and in Pl. 3, fig. 13, rudiments of a fourth
couple.

According to van Beneden, A. lloydii (= A. bournei
Fowler) is distinguished from A. albida by three sets of
characters, well shown in Pl. 3, figs. 1 and 2.   (1) The
relatively small size and shortness of the tentacles, which
are pointed-digitiform and without the terminal pigmental
swellings characteristic of albida.   (2) By the ovoid and
even cylindrical shape of the body.   (3) By the relatively
early appearance of the anterior median marginal tentacle in

A. bournei, which, he says, coincides in time of appearance with the fourth couple of mesenteries. I have, however, a drawing of a specimen of A. bournei, taken at Plymouth in 1914, in which the anterior median marginal tentacle is distinctly represented by a small outgrowth, but only three couples of mesenteries are present, and, as I shall show in the sequel, the time of appearance of the median marginal tentacle is subject to much variation in A. albida. I must add as a fourth distinction, also noted by McMurrich, that the labial tentacles appear earlier and are always more numerous relatively to the number of marginal tentacles present at any stage in A. albida than in A. bournei. Thus in Pl. 3, fig. 3, which is a careful drawing of the youngest stage of A. albida in the Irish collections, and is indeed the youngest yet figured or described, there are distinct indications of the presence of two couples of labial tentacles. In my drawings of corresponding and even later stages of A. bournei from Plymouth there is no trace whatever of labial tentacles.

Beyond these remarks I have nothing to add to our knowledge of A. bournei.

II. The second group comprises three different gatherings made in approximately the same locality, from deep water on the bank stretching out into the Atlantic west of Bantry Bay.

IIA. From Station 31 on August 7th, 1903, fifty miles W.N.W. of Tearaght; Garstang net at 40 fath. Soundings, 306 fath. This sample comprises several hundreds of examples of Arachnactis albida in various stages of development, and has afforded the principal material for this memoir. Unfortunately the catch was not too well preserved, and came into my possession in a screw-stoppered jar, from which spirit readily evaporates; so the histological condition, especially of the delicate younger forms, leaves much to be desired. Some of the older forms, however, are in a tolerably good state of preservation.

IIB. Station 1237, 69 miles W. by N. of Tearaght Light. N. lat. 51° 54′; W. long. 12° 29′. Midwater otter meso-plankton trawl at about 450 fath. Soundings 569 fath.

This gathering comprises six specimens of Arachnactis, of which the largest, obviously much contracted by reagents, measures 4·5 mm. in length × 3 mm. greatest diameter. They correspond very closely to the oldest larvæ figured by Boveri (**5**, Taf. xxi, figs. 5ᵃ, 5ᵇ, 5ᶜ) and, like his specimens, have lost the marginal tentacles almost entirely, but in one of the Irish specimens the attenuated remains of two of the larger marginal tentacles are still attached, and these measure 6·5 mm. from the edge of the oral disc to the tip. These larvæ are opaque ; the general colour of the body in spirit is pink with diffuse dark brown pigmentation in the middle zone.

IIc. Station 1242, August 14th, 1911, 56 miles W. ¼ S. of Great Skellig. N. lat 51° 27′ ; W. long. 11° 51′. Mosquito-net and cheesecloth tow-net on trawl. Soundings, 550–590 fath.

Presumably the trawl was dragged along the bottom at this depth, and the tow-net attached to it was set to catch organisms swimming near the bottom. The catch includes eighteen examples of Arachnactis of various sizes and ages, but all with more than five couples of marginal tentacles. They are obviously identical with the forms taken in catch IIB, and, like them, have in most cases lost the marginal tentacles, a ring of perforations marking the places to which the tentacles were attached. The histology of these specimens was satisfactory. They are undoubtedly A r a c h n a c t i s a l b i d a , M. Sars.

Much has already been written on A r a c h n a c t i s a l b i d a , but as it is of comparatively rare occurrence and inhabits seas not continuously searched by naturalists our information in respect of it still remains imperfect. The most recent account is that of Carlgren (**9**), which follows an excellent summary of our knowledge of the species published six years earlier (**7**). In the latter paper he gives the following definition of the species (translated) : Marginal tentacles long, in earlier developmental stages many times longer than the distance between the oral and aboral ends of the body.

Body discoidal in the younger stages, subsequently more cylindrical with the aboral end rounded off; finally this part becomes pointed. The directive tentacle of the marginal tentacles first appears after the four first marginal tentacle-couples have attained a considerable length, and after three couples of labial tentacles and six couples of mesenteries have been formed. Mesenteries long, in older larvæ reaching nearly to the aboral end; in younger forms the part lying below the actinopharynx (Schlundrohres) is from half to one-third the length of the body. No food-yolk in the larvæ. The aboral pore is formed late (in the stage with twelve labial tentacles [Fowler] or with seventeen tentacles [Boveri]). Colour : Extremities of the marginal tentacles, the actino-pharynx and filaments, brown. Labial tentacles coffee-brown. The remaining parts of the body colourless, transparent. Size : Large form—length of marginal tentacles from 35 to 40 mm. Length of labial tentacles 3–4 mm. Length of body up to 15 mm. Diameter of body up to 7 mm. (in preserved condition).

This diagnosis holds good for the numerous stages that I have been able to examine, with this exception, that I find the time of appearance of the directive marginal tentacle subject to much variation. In some specimens it is distinctly growing out when only two couples of labial tentacles and five couples of mesenteries are present. In other specimens again its appearance is deferred until seven couples of mesenteries are present.

The localities and depths at which the Irish collections were made deserve some attention. Carlgren (7) has given a full list of the localities from which A. albida has been taken up to 1912. Plotting them out on a map, it is obvious that the centre of distribution of this species is north of 57° N. lat., and lies between the Faroe Islands and the Scotch and Norwegian coasts. One catch is reported from as far North as 75° N. lat. and as far east as 32° 18′ E. long. Two catches have been made as far west as 20° W. long. But the few specimens taken by E. T. Browne (6) in Valentia harbour

in 1895 and 1897 and all the specimens taken by the Fisheries Branch of the Department of Agriculture for Ireland come from a restricted area off the south-west coast of Ireland, near 51° N. lat., and thus constitute a more southern sub-centre of distribution. From the fairly constant recurrence of the species in this more southern area (it has been taken there in 1895, 1897, 1903 and 1911), one may surmise that the adult form breeds in the neighbourhood.

In the great majority of cases the species has been found at or near the surface, and sometimes in swarms, as described by Vogt (22) and Vanhöffen (21). Fowler (13), who captured numerous examples in a series of hauls in the Faroe Channel, regarded albida as a purely epiplanktonic form, though he records as doubtful (as regards depth) specimens taken in 300, 400 and 480 faths. But the Danish Ingolf Expedition took specimens at 545 and 625 faths., and, as recorded above, two of the catches now in my possession came from 450 faths. and 550–590 faths. respectively. It is clear that ˙A. albida, in its later stages at any rate, is mesoplanktonic.

As stated above, the catch of 1903 at a depth of 40 faths. contains an abundance of examples of A. albida in all stages of development. I have been able to make a series from an individual with four large and two smaller marginal tentacles and four couples of developed mesenteries up to the individual depicted in Pl. 3, fig. 17, with twelve marginal tentacles and twenty-one mesenteries. Though various authors have described many of the stages included in this series, and Fowler (14) has given a table which includes practically every stage except the oldest, the information is so scattered and the illustrations of the growth periods so incomplete that I propose to give drawings, with brief descriptions of the more important forms that I have studied, which, as I shall show, lead up nearly, if not quite, to the sexual form.

The youngest specimen of A. albida yet figured is that in Carlgren's memoir (7, p. 71, text figure 1ª). The youngest that I could find—and there was only a single example of this stage—is shown in Pl. 3, fig. 3. It is obviously at an earlier

stage than Carlgren's specimen, having four well-developed
and two smaller marginal tentacles; of the latter the right
is, as usual, the larger. Two couples of short, blunt labial
tentacles are clearly present. As shown in Pl. 3, fig. 4, the
body is hemispherical, with the aboral end drawn out into a
blunt projection.

Transverse sections (Pl. 3, figs. 5, 6 and 7) show that this
larva has four couples of mesenteries attached to the actino-
pharynx, and in addition the rudiments of a fifth couple,
represented by two minute ridges in the ventral chamber.
The preservation being indifferent, it is not possible to make
out histological details. Pl. 3, fig. 5, shows that there is
already a differentiation between the epithelium of the sulcus
and that of the rest of the actinopharynx. A thickening of
both ectoderm and endoderm in the directive chamber marks
the commencement of the formation of the directive marginal
tentacle, but there is no outgrowth. Pl. 3, fig. 6, represents
a section taken just below the level of the enterostome. The
section has passed somewhat obliquely from in front pos-
teriorly, so that the hyposulcus is not shown, but this structure
is at this stage extremely short and hardly differentiated.
The two directive mesenteries _d. d._ extend aborally for some
little distance below the hyposulcus. They bear no filaments.
The next three couples, viz. the second and third proto-
mesenteries and the first couple of metamesenteries, bear
filaments. The section portrayed in Pl. 3, fig. 7, passes
through the body just below the bases of the tentacles, one
of which, however, is included, and shows that the proto-
mesenterial couples II and III and the first metamesenterial
couple extend to a considerable distance aborally, but the
directives have disappeared. The second couple is here much
the largest and the filament is enlarged and contorted. At
this stage there is no trace of an acontium on the first couple
of metamesenteries, though, as the figure shows, there is a
slight differentiation of the epithelium of their free edges.
Calling this—the youngest **albida** larva that has yet been
figured or described (unless Fowler's stage A, which he

tabulates as having ten mesenteries, six marginal, and no oral tentacles is of the same age)—stage A, I will describe the older forms contained in the Irish collections as a series of stages B, C, D, etc., taking the number of the mesenteries as the basis of the series.

Stage B (Pl. 3, figs. 8 and 9) has eleven mesenteries—that is, five couples and one member of the sixth couple. There are three couples of long marginal tentacles and a couple of shorter tentacles, of which the right is the larger. The dorsal directive tentacle is represented by a small knob. There are two pairs of labial tentacles, of which the more dorsal couple opens into the third couple of actinocœles,[1] as was first pointed out by Boveri. This form is a little more advanced than Boveri's and a little younger than van Beneden's youngest specimen of A. albida.

Stage C.—Thirteen mesenteries, i. e. six couples plus the developing right-hand member of the seventh couple. Four couples of marginal tentacles, of which the left ventral is markedly shorter than the remainder. In the specimen depicted in Pl. 3, fig. 10, the dorsal directive tentacle is minute, smaller than in the specimen selected to illustrate stage B, but in other examples it is much larger, and nearly as long as the left ventral marginal. Three couples of labial tentacles, the second predominant in size. The body remains discoidal in this stage, and the second couple of mesenteries (counting from the dorsal end) are still predominant in size, and reach furthest down towards the aboral end. The ectodermal musculature of the body-wall is as yet feeble, though that of the tentacles is well developed. In some examples of this stage there are traces of a fourth couple of labial tentacles.

Stage D.—Seven couples of mesenteries, either complete, or the left member of the seventh couple rudimentary. Marginal tentacles nine or ten, viz. four couples of larger

[1] I coin this word as a convenient name for the intermesenterial chambers in a form which, as in Cerianthidæ, has no " exocœles " and " endocœles."

tentacles and generally a very small right member of the
fifth couple, plus the median directive, which varies very
much in development. It may be of considerable size, as in
Pl. 3, fig. 12, but in other examples, such as that shown in
Pl. 3, fig. 13, it may be so small as to be easily overlooked
in a surface view. Three couples of labial tentacles always
present, and in many examples more or less conspicuous
rudiments of the fourth couple.

It is at this stage that important characters begin to make
their appearance, leading from the larval to the sexually
mature condition. The body still remains discoidal, even in
such examples as that shown in Pl. 3, fig. 13, and the
longitudinal musculature of the body-wall is still feeble in
comparison with that of the tentacles. But the column is
beginning to elongate, and it is at this stage that the fourth
protomesenteric couple is first seen to surpass the second
couple in length and to show traces of acontial outgrowths
at the aboral ends. At this stage also a considerable advance
is recognisable in the histological differentiation of the
mesenteries and filaments. The fertile become quite dis-
tinguishable from the infertile mesenteries by the different
characters of their filaments, as seen in transverse section.
The endoderm at the sides of the mesenteries becomes much
thicker, and begins to take on the form characteristic of later
conditions and of the adult Cerianthid, and for the first time
minute but distinct germ-cells may be recognised, forming
clumps in close contact with the mesoglœal lamina of meta-
mesenteries 1. Whilst most of the larvæ at this stage have
the thin, elongated marginal tentacles which give the spider-
like appearance from which the generic name of the larva is
derived, a considerable proportion are found in the condition
represented in Pl. 3, fig. 13, in which the tentacles are
inflated and curved inwards over the oral disc, and the body
is somewhat turgid. Examples in this condition almost
always contain a bolus of food in the actinopharynx, the food
almost invariably consisting of copepods, and this appears to
be the stage at which the larvæ begin to feed freely on other

relatively large-sized planktonic organisms. The increasing histological differentiation is doubtless correlated with the change in the habits of the larva, and the turgid condition of the full-fed forms is a phenomenon familiar to those who have kept and studied living Actinians. They generally become turgid after a meal.

No terminal pore is discoverable in any example of Stage D.

Stage E (Pl. 3, fig. 15).—Eight to $8\frac{1}{2}$ couples of mesenteries. Marginal tentacles eleven or twelve, viz. one directive, now nearly equal in size to the largest of the remainder; four couples of larger and one couple or one and a-half couples of smaller tentacles at the posterior end. Labial tentacles, 4 couples, the last couple small.

The larvæ at this stage have increased considerably in size, and the majority of them are turgid and contain food. The body is now dome-shaped or ovoid and has increased in length. The acontia on metamesenteries 1 are conspicuous, and the mesenterial filaments on protomesenteries III and on metamesenteries 2 are long and much convoluted. At this stage the first couple of metamesenteries is already longer than the third couple of protomesenteries. The actino-pharynx has increased in length, and the hyposulcus is relatively long. Hemisulci are present. The body-wall is as yet thin and its ectodermal muscular and nervous layers feebly developed. There is no terminal pore. Germ-cells, not much advanced beyond those of the previous stage, are recognisable in the first and third metamesenterial couples. This is the earliest stage in which I could detect Carlgren's muscles, i. e. the longitudinal muscles on the posterior faces of the mesenteries in the actinopharyngeal region. A few specimens of this stage occur in the deep water catches; it is very numerous in the epiplanktonic catch.

Stage F (Pl. 3, fig. 16).—Nine couples of mesenteries. Marginal tentacles thirteen, consisting of one large directive, five couples of large and one ventral couple of small tentacles, the right being much larger than the left. Labial tentacles

ten, the last couple very small, and there are traces of a sixth couple.

This stage represents a considerable advance on the preceding. The body is elongated and cylindrical, its walls are thick, and the muscular and nervous layers of the ectoderm are conspicuous. The external ectoderm of the body-wall is now full of the large nematocysts with an irregularly convoluted thread characteristic of Cerianthids. The histological differentiation of the sulcus, hyposulcus, mesenterial filaments and endoderm lining the body cavity is noteworthy. Most conspicuous is the increase in the number and differentiation of the germ-cells. In the first and third couples of metamesenteries there are now numerous ova with a large vesicular nucleus and deeply staining nucleolus. Alongside of these are groups of germ-cells in the nuclei of which mitotic figures are discernible, but the state of preservation did not admit of the study of details of the mitoses. From a comparison with later stages it is probable that these clusters of dividing germ-cells are destined to give rise to spermatozoa. The terminal pore is now present, and its time of appearance seems to coincide with the full development of the ectodermic musculature of the body-wall. The pore and the strongly developed muscles are doubtless correlated, the pore serving to relieve the internal pressure set up when the walls of the body are powerfully contracted.

Stage F is abundant in the epiplanktonic catch and also occurs in the mesoplanktonic deep-water catches.

Stages G and H.—I class under these all forms with nineteen or twenty (stage G) and twenty-one (stage H) mesenteries. In other respects there is very little difference between these two last stages. They have generally from sixteen (stage G) to eighteen marginal tentacles and ten labial tentacles. They all show fully developed Cerianthid characters, with a thick body-wall having strongly marked muscular and nervous layers—a well-marked terminal pore, and in all two couples of mesenteries, viz. the first and third couples of metamesenteries, bear gonads in a more

or less advanced stage of development. These stages occur in both the epiplanktonic and meso-planktonic catches, but are relatively scarce in the former and predominant in the latter. Pl. 3, fig. 17 shows the largest and most complete example taken in the epiplanktonic catch. It is obviously much contracted in spirit and its total length is only 17 mm., the body measuring 9 mm. in length with a diameter of 2 mm. This particular example has all its marginal tentacles intact, and for this reason was chosen for illustration, but it is probably only an early condition of stage G. In the corresponding and later stages in the epiplanktonic examples the marginal tentacles are in the process of being cast off, and more or fewer are always missing. The contents of the jar consisted largely of cast-off tentacles. The mesoplanktonic examples have without exception cast off their marginal tentacles, only attenuated threads remaining here and there in a few cases. After examining with some care the cast-off tentacles and the scars marking their former attachment to the edge of the oral disc, I have come to the conclusion that the marginal tentacles in this species are autotomous, and are normally cast off when the animal approaches sexual maturity and descends from the epiplankton down to the depths. One reason for this opinion is that the edges of the scars, which are really perforations leading freely into the actinocœles, are not ragged as they would be if the tentacles had been torn off in the net, or as a consequence of the rapid change of pressure in the course of the ascent from deep water to the surface. On the contrary, there is a thickening of the mesoglœa all round each perforation, and the ectoderm passes as conformably into the endoderm at the edges as it does, for instance, in a mesenterial filament. Secondly, the cast-off tentacles show no signs of rough usage, but are mostly plump and retain their shapes, but in every case there is a marked constriction, deep enough to close the tentacular cavity, at the basal end, indicating a violent local muscular contraction which has severed the tentacle from its attachment. Thirdly, there is

the consideration that these large marginal tentacles are clearly the organs of locomotion of the epiplanktonic phase of existence ; from their inflated character it may be inferred that they function largely as hydrostatic organs, and they would not only be useless, but actually a hindrance to the descent of these organisms into deep water at the onset of sexual maturity.

For there is no longer any doubt that the deep-water forms are very nearly, though I cannot say quite, sexually mature, and I can corroborate and amplify Vanhöffen's (**21**) observations and remarks on this subject. I may say in this connection that it seems to me very probable that the floating actinian captured and figured, but subsequently lost, by Vogt, was really an Arachnactis albida in stage G or H. It is true that Vogt's drawing, made on board ship under conditions unfavourable for study, is obviously inaccurate. The smaller tentacles, which may be taken to represent the labials, are attached to nowhere in particular, and there are other obvious errors. But Vogt's figure bears so close a resemblance in outline to Vanhöffen's careful drawing, and the locality and conditions under which Vogt made his capture agree so well with all that we know of the distribution and habits of Arachnactis, that I cannot agree with the summary manner in which Boveri (**5**) dismissed this form as clearly belonging to some other genus, albeit subsequent authors, with the exception of Vanhöffen, have nearly universally accepted Boveri's criticism. On the other hand, it seems to me extremely improbable that Vogt really saw ciliated larvæ within the body-cavities of his specimens. What he probably saw was a bolus of food kept in motion by the cilia of the filaments. In several of my specimens there is a globular mass of half-digested food which, at a first glance, might well be mistaken for an embryo in the living form.

Vanhöffen described and figured, but none too exactly, ova in the fertile mesenteries of his specimens. As he only describes and figures fifteen marginal tentacles his examples cannot have been much older than my stage F, in which, indeed,

developing ova are distinguishable, but not far advanced.
Fowler states briefly that generative cells make their first
appearance in his stage I, with nineteen mesenteries and some
fourteen marginal tentacles. I have already shown that they are
recognisable at a much earlier period. What is of more impor-
tance is that in my stage H, with twenty-one mesenteries, I have
found both ova and spermaries, as shown in Pl. 4, fig. 21.
The drawing (which does not include ova of the largest size)
shows that the ova at this stage are in a fairly advanced stage
of development with large pale vesicular nuclei, a sparse and
feebly staining chromatic reticulum and a large deeply stained
nucleolus. The spermaries are evidently immature, and the
cells in them may be regarded as spermatogonia. In no
case have I found ripe spermatozoa. These examples, all of
which came from the deep-water catches, are therefore not fully
sexually mature, though more advanced than any specimens of
A. albida yet recorded. One would say that they cannot be
far removed from sexual maturity, and the question arises
whether these deep-water stages which have cast off their
marginal tentacles and have twenty to twenty-one mesenteries
may be regarded as the adults of Arachnactis albida?
It is no longer possible to dismiss this question summarily, on
the ground that these forms are pelagic and that all sexually
mature and adult Cerianthids are sedentary, for we now
know that this generalisation is incorrect. Gravier (15)
has described in detail, under the name of Dactylactis
benedeni, a pelagic Cerianthid taken by M. Léon Diguet in
the Gulf of California. He is explicit: the spermaries in his
examples contained ripe spermatozoa, so there can be no
doubt that this species is sexually mature, and yet an epi-
planktonic form, for it is expressly stated of M. Diguet's
collections that they " nageaient en nombre considérable dans
les couches superficielles, à la surface même ou à une faible
profondeur .   .   .; la plupart d'entre eux possèdent des
éléments reproducteurs complètement développés ou très
voisins de l'état de maturité."

It would therefore be reasonable to claim that the meso-

planktonic and nearly sexually mature forms taken at depths of 450 and 550 fathoms off the coast of Ireland in 1911 represent the hitherto unknown adult form of Arachnactis albida.

But Carlgren (9) has pointed out close resemblances between the older forms of A. albida and a sedentary Cerianthid dredged from a depth of 140 fathoms in the Trondjhem Fiord, and named by him Arachnanthus sarsi. Without committing himself to a definite assertion, Carlgren considers that it is highly probable that Arachnanthus sarsi is the adult form of Arachnactis albida.

He gives the following critical characters in his diagnosis of A. sarsi (loc. cit. p. 27):

(1) Stomatodæum of medium length, with very long hyposulcus that reaches past the middle of the animal and exceeds the stomatodæum in length.

(2) The directive mesenteries comparatively long, but extending further than the middle of the hyposulcus.

(3) Protomesenteries of the second cycle of the length of the hyposulcus, probably sterile, without cnido-glandular tract.

(4) Protomesenteries III about the length of the directive mesenteries, with very short ciliated tract region and a very long cnido-glandular tract region.

(5) The metamesenteries of the second cycle almost as well developed as those of the first.

(6) The oldest mesenteries of the first and second cycle long, reaching not quite down to the aboral end of the animal, fertile, with long ciliated-tract region. The first metamesentery on each side with an acontium.

(7) The metamesenteries of the third (B) and fourth (b) cycle short, about the length of protomesenteries 3, sterile, with very short ciliated-tract region and very prolonged cnido-glandular tract; b slightly shorter than B.

(8) The musculature of the mesenteries comparatively well developed.

I have examined fifteen examples of Arachnactis albida with from eighteen to twenty mesenteries and five or six

couples of labial tentacles, some by transverse sections and others by dissections, such as that shown in Pl. 4, fig. 19, and find the following points of agreement and difference between this species and Arachnanthus sarsi:

(1) The hyposulcus, or, as I shall call it in future, the hyposulculus, in A. albida reaches past the middle of the animal, but is very variable in length relatively to the actinopharynx (stomatodæum). Usually it is of about the same length; it may be a trifle longer, but is as often decidedly shorter. These differences obviously depend on the state of contraction of the example under observation.

(2) In all my examples the directive mesenteries extend to, and are somewhat prolonged beyond, the aboral end of the hyposulculus. This is a difference of capital importance.

(3) In A. albida protomesenteries II are always considerably longer than the hyposulculus, are sterile, but have a well-marked cnido-glandular tract forming a compact coil at their aboral extremities. This is a constant feature, and the transition from the ciliated-tract region to the cnido-glandular tract region can clearly be seen in sections. This is a second distinction of capital importance between Arachnactis albida and Arachnanthus sarsi.

(4) In A. albida protomesenteries III are decidedly longer than the directives, reaching aborally about as far as the end of the ciliated-tract region of protomesenteries II.

(5) In this feature A. albida agrees with Arachnanthus sarsi, and also generally in 6, 7 and 8.

The differences are sufficiently great, yet there are many points of resemblance. In Arachnanthus, as in my oldest examples of Arachnactis albida, there are twenty-one mesenteries, and in both species the three smallest do not bear filaments. In both species there is no labial tentacle over the directive actinocœle, nor over the two adjacent actinocœles. In both there is a well-developed acontium at the aboral ends of the first couple of metamesenteries. Further, it is worthy of notice that the single known example of Arachnanthus sarsi had no trace of tentacles, and I

have shown that, as they approach sexual maturity, the larger
forms of Arachnactis albida lose their marginal tentacles,
and, as it would seem, sink to considerable depths, there to
become fully mature. In most of my examples the labial
tentacles were present and conspicuous, but in one or two of
the largest taken in deep water these had also disappeared—
whether torn off or cast off I am unable to determine.

From the evidence before me I think I am justified in
constructing the following life-history of Arachnactis
albida : The youngest larvæ appear at about midsummer
and are epiplanktonic, swimming at or near the surface by
the aid of their long tentacles (Vanhöffen, **21**). As is commonly
the case in epiplanktonic organisms, they appear in shoals, in
this differing from A. bournei, which in my experience
never appears in shoals, but forms a somewhat infrequent
element in epiplanktonic catches, and is taken in small numbers
at a time. At first of small size, the larval A. albida grows
rapidly, and on arriving at a stage with thirteen to fourteen
mesenteries and ten marginal tentacles it feeds greedily on other
organisms of the epiplankton, chiefly copepods, in the late
summer months. Towards the onset of autumn it has attained
nearly its full growth, having fifteen to eighteen marginal and
ten to twelve labial tentacles, with twenty to twenty-one mesen-
teries. It then throws off its marginal tentacles and sinks towards
the bottom, and by the time that it has reached a considerable
depth its ovaries and spermaries are in a fairly advanced
stage of development. It is adolescent, if not fully adult.
This brings us to the autumn months, and it remains a matter
of conjecture what form it assumes and what is its habitat
during the winter. That it enters upon a period of winter
rest can hardly be doubted, for the young larvæ do not
reappear until the following spring. We do not know
whether it buries itself in the sea-bottom, as do other
Cerianthids, or whether it remains as an element of the
mesoplankton near the bottom—more probably the latter, as
no examples have been recorded as taken by the dredge in so
well-explored an area as the banks off the south-west coast

of Ireland. However this may be, it seems certain that it develops its ova and spermatozoa—like most other Cerianthids, Arachnactis albida is monœcious—in the warmer waters of considerable depths during the winter months, and in the spring the fertilised ova are discharged and the developmental cycle begins again.

If I am right in claiming, as I do, that the deep-water examples with twenty to twenty-one mesenteries, ten or twelve labial tentacles, a thick ectodermic musculature and gonads in a fairly advanced stage of development, are the adult forms of Arachnactis albida, and undergo little further change beyond the ripening of the sexual products, then this species is certainly not identical with Arachnanthus sarsi, as described by Carlgren. The differences in the protomesenteries, recorded above, are sufficient to separate the two. At the same time the resemblances are many, and one cannot doubt the correctness of Carlgren's conclusion, that "A. albida is a larval form falling under the same genus as Arachnanthus, which cannot be said of Arachnactis bournei and brachiolata." It is possible that the discovery of new examples of Arachnanthus sarsi may result in the disappearance of the anatomical differences which at present separate it from A. albida. Carlgren tells us that he "did not like to dissect fully the one specimen he had for study, especially as the mesenteries were not very well preserved." As the differences noted depend on mesenterial characters, further and better opportunities for study may show that they are non-existent.

But the possibility must not be ignored that the larvæ and adult or quasi-adult forms taken off the south-west coast of Ireland belong to a species or sub-species distinct from A. albida. In the first place, they come from a well-defined area several degrees south of the equally well-defined area of distribution of the more northern forms. Secondly, there is a considerable disparity in size. The largest examples taken by Vanhöffen measured, after preservation in spirit, 15 mm. in length of body; the marginal tentacles measured 35 to

40 mm. in length. The largest examples from the Irish collections measure 9 mm. in length of body, with a tentacle length of 22 mm. Thirdly, I could not find any trace of the deep, chocolate-brown coloration of the labial tentacles and actinopharynx described by Vanhöffen for A. albida, and also characteristic of the mouth and actinopharynx of Arachnanthus sarsi. The colour may have been dissolved out in spirit, but the body-walls retain a considerable amount of brown pigmentation, and if it persists here, why not in the labial tentacles? In all my specimens these latter are brilliantly white. There are also small anatomical and histological differences, to which I shall refer further on, and all these facts taken together warrant my describing the Irish forms as a distinct variety or subspecies under the name Arachnactis albida var. hibernica, with the characters enumerated above. I am further of the opinion that the differences in size, colour (?), distribution and minute anatomical detail are accompanied by a change of habit, and that the evidence at our disposal points to the conclusion that the adult hibernica does not bury itself in the sand, but remains a member of the mesoplankton during the ripening of its sexual products and to the end of its individual existence, which I opine terminates with the discharge of its ova and spermatozoa. In support of this view, I may remind my readers that some of the largest and most mature examples in my possession were taken in a mesoplankton net at a depth of 450 fathoms, but 111 fathoms from the bottom of the sea.

If I am right in this opinion, the life-history and habit of hibernica is intermediate between that of the epiplanktonic Dactylactis benedeni described by Gravier and that of Arachnanthus sarsi, supposing the last-named to be, as it most probably is, the adult form of Arachnactis albida. In his classical memoir on Cerianthid larvæ van Beneden has recorded the presence of germ-cells in Dactylactis armata and in Ovactis brasiliensis. In the latter species they are in a very early stage and no better developed than in my

stage D of Arachnactis, but in the former species they are of sufficiently large size to indicate the approach of sexual maturity. I venture to predict that it will be found that several of the pelagic Cerianthids attain the adult condition whilst still epiplanktonic, others passing from the planktonic to the more typical sedentary habit of adult Cerianthids. If this be so—and we now know of at least one case in Dacty-lactis benedeni—it is only consistent with analogous phenomena in not very distantly related organisms—the Hydrozoa. In this group, as Weismann showed, the increasingly early development of the sexual products has led to a parallel change of habit in several families of the Hydroids, the advantage gained by early maturity more than compensating the disadvantage involved in the suppression of the free-swimming Medusa stage, whereby the ova were widely distributed. In the Cerianthids, the advantage gained by early maturation of the sexual products leads to a change of habit in an inverse direction. It is the sedentary form that is in process of elimination, whilst the pelagic phase assumes increasing importance. In instituting this comparison, I do not forget that Dactylactis benedeni, with its long directive mesenteries, acontia on the third as well as on the first couple of metamesenteries, and labial tentacles in the actino-cœles adjacent to the directive, is structurally different from Arachnactis, and cannot be regarded as forming part of the same evolutionary series. But this is only consistent with the changes observed in Hydroids, in which group parallel changes are observed in the life-histories of several different families.

ANATOMY AND HISTOLOGY.

This subject has been dealt with in great detail by van Beneden (3 and 4), Vanhöffen (21), and more lately and most fully by Carlgren (8 and 9). Though I have a few observations to offer, I shall not attempt to traverse all the ground that has already been so thoroughly explored.

Symmetry and Orientation.—It is necessary to justify and explain the position I have taken up and the terms that I have selected for use in the preceding pages, because previous authors differ very much from one another on these matters. Only recently, McMurrich (**18** and **19**) has given lengthy and most respectable arguments in favour of using the terms " dorsal " and " ventral " in a sense exactly inverse to that in which they are used by Carlgren. I have never found myself able to accept the homology, originally propounded by Caldwell and Sedgwick, and vigorously supported by van Beneden as a consequence of his researches on the development of Cerianthiaria, between the successively formed actinocœles of the Anthozoa and the paired and unpaired cœlomic cavities of Annelids and Chordata. The arguments advanced in support of this hypothesis are extremely ingenious, and have a great attraction for those who conceive it to be the province of the zoologist to construct a system of speculative phylogenies. But whilst recognising the intellectual pleasure derived from this form of mental exercise, I cannot but regard it as altogether outside the domain of reality. The arguments brought forward are not susceptible of proof or disproof; they are only capable of sustaining a greater or less amount of probability, and when pushed to an extreme, the improbability largely preponderates over the probability. The "architectonic"—to borrow a word from German authors—of the Anthozoa and such phyla as the Annelida and the Chordata is so fundamentally different; the final result of the developmental history is so radically dissimilar, that I am convinced that we are dealing with things which, as the logicians say, are not in pari materiâ, and I cannot regard speculations as to the common origin of their characteristic structures as serious contributions to science, the more so because we are learning daily, from the school of genetics, that imaginary evolutionary series, apparently founded upon a series of demonstrated facts, break down altogether when confronted by the actual sequence of events as proved by experiment. The human intellect, how-

ever powerful and imaginative, is not only liable but certain
to err in the attempt to reconstruct in detail long lost series
of sequences, and I am disposed to say of this form of
zoological speculation what Roger Bacon said long ago of
other philosophical works: "Non est nisi amissio tem-
poris studere in illis et multiplicatio ignorantiæ et
causa erroris."

For this reason I must discard van Beneden's identifica-
tion of anterior and posterior, dorsal and ventral surfaces.
It does not correspond to the natural position assumed by the
animal, for Arachnactis does not swim, as van Beneden
supposed, mouth downwards, but mouth upwards. Thus
Vanhöffen says: "Die weissen runden Randtentakeln mit
bräunlicher Spitze sah man weit ausgebreitet an der Ober-
fläche des Wassers während der rübenförmig langgestrechte
oder kugelig contrahirte Körper senkrecht dazu herabhing."
It is better, I think, to adopt the conventional orientation
originally proposed by Kölliker, and to use the terms
" dorsal " and " ventral " in the sense adopted by him. I
should have preferred to adopt a more logical system and to
make use of the descriptive terms " sulcar " and " sulcular "
to define the opposite ends of the long axis of the actino-
pharynx, as I proposed many years ago, but the majority of
authors seem to prefer the conventional though meaningless
nomenclature, and it is best to conform to the prevailing
practice.

The question then arises which is the " dorsal " and
which the " ventral " aspect of a Cerianthid? I have no
hesitation in ranging myself on the side of Carlgren,
McMurrich's special pleading notwithstanding. The single
œsophageal groove of Cerianthids is " dorsal," and the
opposite aspect, where new metamesenteries are added, is
" ventral." Hence the œsophageal groove of Cerianthids
corresponds to the sulculus, not to the sulcus, of Hexactinians,
and I have called it by that name. Is not Carlgren himself
inconsistent when he applies the name " siphonoglyph " to the
dorsal groove of Cerianthids? The term " siphonoglyph " was

invented by Hickson to denote the ventral groove of Alcyonarians. For the rest, Carlgren's argument on this subject appears to me irrefutable, and it is not necessary for me to repeat it. I only take this opportunity of stating that I fully confirm his account of the arrangement of the musculature on the faces of the mesenteries in Arachnactis. The longitudinal muscles are on the ventral faces of all the mesenteries, including the directives. I had made drawings illustrating this point, but they so precisely resemble Carlgren's (**9**, tab. v, fig.. 8) that it is not worth while to publish them.

Having settled the use of the terms " dorsal " and "ventral" it is necessary to explain my use of the terms " right " and " left." I use them in a purely descriptive sense, the animal being supposed to be placed mouth upwards with the dorsal or sulcular aspect furthest from the observer. They thus correspond with van Beneden's use of them, but without any implication as to anterior and posterior extremities.

Lastly, I am in full agreement with Carlgren's view that the first three couples of mesenteries, counting from the dorsal side and including the directives, are the primary or protomesenteries, and that all the succeeding couples are secondary or metamesenteries. His arguments in favour of this view seem to me unassailable.

The Mesenteries.—As regards their general arrangement, succession, and differentiation into alternate fertile and infertile couples, I can only confirm the accurate observations of Boveri, Faurot, van Beneden and Carlgren: Vanhöffen's attempt to demonstrate an entirely different sequence of mesenterial development to that described by Boveri and van Beneden has already been sufficiently criticised by the two last-named authors. As I have pointed out, the full histological differentiation of the mesenteries begins at the close of stage C, and is nearly complete in the protomesenteries and in the first couple of metamesenteries in stage D. Prior to this the mesenterial filaments, excepting those of

protomesenteries II, are not more differentiated than they are in the second and third couple of metamesenteries as shown in Pl. 4, fig. 20. It will be noticed in this figure that the endoderm on the lateral faces of the mesenteries is still very thin. It is at this stage that I find the first evidence of the larvæ beginning to feed on Copepods, and immediately afterwards the endoderm takes on what may be called its adult character, and consists of very long highly vacuolated cells, with various inclusions, such as nematocysts and trophocytes, which I shall deal with further on.

The section in Pl. 4, fig. 20, passes through the hyposulculus, to which the directive mesenteries are attached. The second couple of protomesenteries have the characteristic T-shaped filament of the ciliated-tract region. Of the third couple of protomesenteries the section through the right-hand member passes through the ciliated tract region, which, it will be observed, is slightly different in outline from the corresponding region in the second couple of protomesenteries. On the left hand, the section passes through the cnido-glandular tract region of the third couple of protomesenteries. The first couple of metamesenteries have conspicuous T-shaped filaments, but the second and third couples of metamesenteries have as yet small and undifferentiated filaments.

Without going into further details, I can confirm all that previous authors have observed. As successive couples of metamesenteries are added in the ventral actinocœle they are differentiated into alternate fertile and sterile couples, the couples bearing an odd number being fertile, those bearing an even number, sterile. The two kinds can easily be distinguished, at a short distance below the enterostome, by the different shape of the filaments in cross section. The filaments of the fertile mesenteries are invariably T-shaped and the angles formed by the limbs of the T are lined by relatively large cubical cells, with large deep-staining nuclei, and bearing long cilia. These are the " ciliated tracts " of the authors, but a more appropriate name would be " ciliated grooves." In all my examples with sixteen mesenteries and

upwards I have found germ-cells, in a more or less advanced
stage of development, in the first and third couple of meta-
mesenteries, very early germ-cells in the fifth couple of
metamesenteries, but none in the second couple of proto-
mesenteries.   I have also noticed a distinction which seems
to have escaped the attention of other observers.   In the
second couple of protomesenteries and in all the meta-
mesenteries designated by an odd number, except the very
youngest, the lateral endoderm of the mesenteries contains
large sausage-shaped nematocysts, different from those occur-
ring in other parts of the body.   The alternating couples of
mesenteries, i. e. the sterile couples, are altogether devoid of
these nematocysts.   By way of contrast I have placed one of
these nematocysts alongside two large nematocysts, one from
an acontium, the other from the cnido-glandular tract of a
filament, in Pl. 3, fig. 18 A, B and C.   The nematocysts from
the endoderm of the second couple of protomesenteries and
from the fertile metamesenteries are half as long again as
the others, are curved, and the axial thread and spiral filament
are placed eccentrically nearest the convex side of the
capsule.   They stain bright green in picro-indigo-carmine,
the capsule and its contents of a transparent light green,
the thread and axis darker green, and are very conspicuous
objects.   In sections stained with hæmatoxylin and eosin they
are coloured pink, but are not so clearly differentiated as by
the picro-indigo-carmine stain.   What their function and
significance may be I cannot tell, but since they are con-
stantly present in certain couples of mesenteries and as
constantly absent in the other alternating couples, they must
be correlated in some way with the other structural and
physiological characters that distinguish the alternate couples.
The only other general remarks that I have to make about
the mesenteries are the following:

The directive or first protomesenterial couple are short, but
continued a short distance below the lowest limit of the
hyposulculus, and are attached to the short hemisulci.   I
confirm Carlgren's observation that the so-called filaments on

these mesenteries are really continuations of the hemisulculi : in fact " hemisulculus " is only another term for the somewhat specialised filament of the directives. Below the hemisulculi the directives have no filament, nor even a craspedion. Their edges are covered by slightly enlarged but otherwise undifferentiated endoderm cells.

The second couple of mesenteries has a very long ciliated-tract region, extending far below the lowest limit of the hyposulculus, towards the aboral end of the body. This ciliated-tract region is quite straight in fully expanded examples, but in contracted examples may be so sinuous as to resemble the convolutions of the cnido-glandular tract-region. At their aboral extremities the ciliated-tract region of the second protomesenteries passes abruptly into a cnido-glandular tract region, which forms a conspicuous and compact coil. The protomesenteries of the second couple never contain germ-cells, but, as I have observed, always exhibit the large sausage-shaped nematocysts in the endoderm covering their faces. This couple is in many ways intermediate between the fertile and sterile couples of the metamesenterial series, and it is perhaps a legitimate speculation that in some ancient " Cerinula " ancestral form with only three couples of mesenteries they were the fertile couple, but have since lost this function.

The third couple of protomesenteries has a short ciliated-tract region and a long, much convoluted, cnido-glandular tract region. They are of constant length, reaching aborally as far as the ciliated-tract region of the second protomesenterial couple. The first couple of metamesenteries is the longest in the body, extending nearly as far as the aboral pole. These mesenteries are always fertile, have a very long ciliated-tract region, normally straight, but puckered into numerous coils in contracted examples; no cnido-glandular tract region, and they end in the short digitiform offsets generally known as acontia.

The second couple of metamesenteries have the same structure as the third couple of protomesenteries, and are

about as long as the latter. In some sectional series they appear to be rather longer.

The third couple of metamesenteries is, if anything, a trifle longer than the second couple. It is always fertile, and, saving that it has no acontia, is in every respect similar to the first couple.

The fourth couple of metamesenteries is scarcely more than half as long as the second couple, is sterile, and presents the same characters as the last-named. The sixth couple is similar, but extends a very little way below the enterostome and has a very short cnido-glandular tract.

The fifth couple of metamesenteries is shorter than the fourth, and does not contain developed germ-cells in any of my preparations. But it is possible to detect clumps of cells either closely adherent to, or included within, the mesoglœal lamina, and as these exhibit mitotic figures, they are doubtless early germ-cells. This couple of mesenteries probably becomes fertile in individuals older than any that I had for examination.

In examples in which the seventh and a member of the eighth couple of metamesenteries were present, these did not extend down to the level of the enterostome and showed no trace of filaments.

The Mesenterial Filaments.—These structures, as seen in A. albida, were concisely and accurately described by Fowler (13) in 1897. More recently Carlgren (19) has studied them in great detail, giving a comparative account of their histology in different genera and species of Cerianthidæ, and dealing with the nomenclature of the various regions into which a filament, whether of a fertile or sterile mesentery, can be divided according to its histological characters. I have not found this account easy to follow. The facts are correctly described, but the terms "region," "tract," "streak" and "groove" are so loosely defined and so capriciously applied that the meaning is often obscure. I venture to apply a revised and exact nomenclature to a summary of Carlgren's exposition. The name "craspedon" was originally

given by Gosse to the whole mesenterial filament of an
Actinian. It is derived from the Greek κράσπεδον, an edge
or hem, and on etymological and other grounds it is better
to use it in its original signification rather than limit it to
any specialised part of a filament. At a later date the
brothers Hertwig (17) demonstrated that a craspedon has
not a uniform structure throughout, but differs in histological
and other characters in the oral, the middle and the aboral
regions of its course. In the Cerianthidæ the more aboral
region is straight, or nearly so. This may be called the
orthocraspedon. There follows a much coiled region, to which
the name "plectocraspedon" (πλεκτός, twisted) may be given.
The terminal or most aboral region, if it has special cha-
racters, may be called the "telocraspedon."

The Hertwigs further described three longitudinal streaks,
stripes or tracts in the craspedon. A middle "Drüsenstreif,"
afterwards known as the cnido-glandular tract, and on either
side of it a "Flimmerstreif," afterwards known as the ciliated
tracts. It will save confusion if the term "tract" is strictly
limited to these linear differentiations of the epithelium of
the craspedon, and if we limit the term "region" to the
three above-named divisions—the ortho-, plecto- and telo-
craspedon.

Carlgren shows that in Cerianthidæ the most oral region
in all the mesenteries, excepting the directive mesenteries
which have no true filament, is similar in structure, though,
as described above, it varies considerably in length in the
various couples. This orthocraspedon is more differentiated
histologically than the Hertwigs or even Fowler described,
and may be subdivided, as is shown in Pl. 5, fig. 24, into a
middle portion, composed almost exclusively of granular
columnar epithelial cells, each bearing a single flagellum and
two lateral portions, in which spirocysts and glandular cells
predominate. Carlgren calls the whole of the middle tract
the "median streak," and subdivides it into a middle and
two lateral portions, but proposes, as an alternative, the name
"spirocyst-glandular tract." Alternative names are objec-

tionable, and it will be well to adopt and use only the term
" spirocyst-glandular tract." The orthocraspedon in the
Cerianthidæ is straight or at the most slightly sinuous; its
median tract is a spirocyst-glandular tract, and the two
lateral ciliated tracts always co-exist with the last-named. It
forms the oral region of all mesenteries except the directives,
is very long in protomesenteries II and in metamesenteries
1, 3, 5, but is short in protomesenteries III and in meta-
mesenteries 2, 4, etc.

Macroscopically the region of the plectocraspedon is
conspicuous by the convolutions into which it is thrown ;
microscopically it is characterised (1) by the absence of the
lateral ciliated tracts ; (2) by the character of the middle
tract, which is more or less tongue-shaped in section, and its
epithelium contains an abundance of large, coarsely-granular
gland-cells, and the spirocysts are replaced by large, thick-
walled nematocysts of the type shown in Pl. 3, fig. 18B,
almost to the exclusion of the former. For this Carlgren
reserves the name " cnido-glandular tract," and though there
is a certain inconvenience in thus limiting the significance of
a term originally used in a more general sense, it will be best
to follow him. In sections stained with picro-indigo-carmine
or with hæmatoxylin and eosin, the cnido-glandular tract
stands in sharp contrast to the spirocyst-glandular tract. In
the former the gland-cells are highly eosinophilous or stained
bright green with picro-indigo-carmine, whereas the gland-
cells of the lateral areas of the spirocyst-glandular tract are
but feebly eosinophilous and give a light indigo-blue colour
with picro-indigo-carmine.

The telocraspedon is the aboral region in which only a
spirocyst-glandular tract remains, the lateral ciliated tracts
having disappeared. It corresponds to the " craspedion "
region of Carlgren. In Arachnactis albida, as a rule,
mesenteries that have plectocraspeda, viz. protomesenteries
II and III and metamesenteries 2, 4, etc., have no telo-
craspedal region, and vice versâ, those that have telocras-
peda, viz. metamesenteries 1 and 3, have no plectocraspeda.

But in one of my series the left member of the first meta-mesenterial couple has a very short convoluted region some way above the acontium, and this has in part the characters of a plectocraspedon in that it exhibits the large, thick-walled nematocysts and eosinophilous gland-cells characteristic of the latter region. This exceptional differentiation, however, is absent from the other member of the couple. Carlgren tells us that the telocraspedal region co-exists with the plecto-craspedal in certain mesenteries in Cerianthus lloydii, vogti and americanus, and in all the mesenteries but the directives in Botrucnidifer norvegicus.

Carlgren (**9**, text-figs. 8, 9, 10, p. 61) describes and figures transverse sections through the orthocraspeda of Arach-nactis albida, Cerianthus lloydii and Botrucnidifer norvegicus, and says that there is a regular gradation in the form of the mesoglœal lamella where it broadens out in the craspedon in these and other Cerianthids. I cannot speak for species which I have had no opportunity of examining, but would point out that at least two of his grades are represented in Arachnactis albida. Pl. 5, fig. 24, is a careful drawing of a section through an orthocraspedon of a fertile mesentery (metamesentery 1) in this species. It has all the characters shown in Carlgren's text-fig. 9, and stated by him to be characteristic of the species. But Pl. 5, fig. 25, is a drawing of a section through a sterile mesentery of the same individual as that from which Pl. 5, fig. 24, is taken, and it has much more nearly the characters of Carlgren's text-fig. 8, which he describes as characteristic of Cerianthus lloydii. A further reference to Pl. 4, fig. 20, shows that in newly-developed mesenteries the shape of the spirocyst-glandular tract and the club-like termination of the mesoglœal lamina nearly resembles the condition said by Carlgren to be characteristic of Botrucnidifer norvegicus, so all three grades, and, indeed, many intermediate ones, are represented in one species—A. albida. Generally, in A. albida, the orthocraspeda of the sterile mesenteries have the appearance in transverse section shown in Pl. 5, fig. 25, those of proto-

mesenteries II and the fertile metamesenteries are broader, and the spirocysts and gland-cells are more distinctly grouped at the edges of the spirocyst-glandular tract, as shown in Pl. 5, fig. 24. But the actual shape varies very much according to the state of contraction. Very commonly the edges of the spirocyst-glandular tract are turned up so as to enclose a deep groove lined by the ciliated cells of the central portion, and in another part of the same craspedon the edges are depressed as shown in Pl. 5, fig. 24. The shape and relative thickness of the mesoglœal lamina also varies with the state of contraction, and if, as I think is the case, the mesoglœa itself is contractile, or at any rate very plastic and liable to great changes of shape as a result of the contraction of adjacent tissues, it is evident that no reliance can be placed on the form of the orthocraspedon as a specific criterion.

Carlgren also deals at some length with the origin of the craspedon, and subscribes to the opinion already expressed by Fowler and others, that not only the spirocyst-glandular and cnido-glandular tracts, but also the lateral ciliated tracts, are direct continuations of the actinopharyngeal epithelium, and therefore ectodermic. The ciliated tracts, he says, are direct continuations of the actinopharyngeal furrows, of which the cells lining the deeper parts of the grooves change their character in the most aboral part of the actinopharynx and take on the character of the cells of the ciliated tracts. At the point of departure of the mesentery from the lower edge of the actinopharynx, the modified ectoderm in the bottoms and a portion of the sides of the furrows of the latter passes over into the ciliated tracts. As I have argued that the analogues of the ciliated tracts and also the acontia of the micromesenteries of Decaphellia psammomitra are endodermal in origin, I have paid special attention to this point. The facts are as Carlgren describes, but the actual conditions not quite as simple as would appear from his description and figures (loc. cit., tab. iv, figs. 1, 2 and 3). The so-called enterostome of Arachnactis, and of Cerianthids in

general, is not a simple opening at the bottom of a tubular actinopharynx, but the walls of the latter diverge from the mid-ventral line like the folds of a pair of curtains, and the edges of the folds are both festooned and everted in such wise that their edges are turned up and project into the actinocœles. This is illustrated in Pl. 5, fig. 26, which is a tracing of a section cutting through the descending wall and the upturned lower edge of the actinopharynx. The outer face of the latter is covered by bands of modified ciliated cells, here indicated by a thick black line. The details of these cells are given in Pl. 5, fig. 29.

Pl. 5, fig. 27, is a drawing of a section somewhat lower down which passes near the edge of the fold of the upturned actino-pharyngeal wall. The bands of ciliated cells are interrupted at the points where the furrows of the actino-pharynx are curving round its everted lower edge. In Pl. 5, fig. 28, the actinopharyngeal ridges are passing into the craspeda and are separate from one another. The groove-shaped ciliated tracts formed by the disconnected portions of the ciliated band are now apparent. Inter alia these sections show the shift of the attachments of the mesenteries from the grooves to the ridges of the actinopharynx as van Beneden described.

It is evident that the bands of ciliated cells mark the line where the ectoderm passes into the endoderm, and if we follow them down the craspeda as the ciliated tracts, we always find them forming the boundary line between the two germinal layers. Eventually, in the region of the plecto-craspedon and telocraspedon, they die out and the boundary-line becomes indistinct. These relations may be understood by reference to the diagram Pl. 5, fig. 30, in which the lighter tone represents the endoderm, the darker tone the ectoderm; the thick black line represents the modified epi-thelium of the ciliated tract, and the broken lines the insertions of the mesenteries on the actinopharynx and craspeda. One half of the animal is represented, the actino-pharynx with its everted rim being completely flattened out

in one plane. Whether the modified cells of the ciliated tracts should be referred to ectoderm or endoderm is an open question, and perhaps of no very great importance. What is clear is that they indicate the boundary-line between the two layers, and if there is an invaginate gastrula in the Cerianthids—a matter on which we have no exact information —they may be regarded as a differentiation of the lip of the blastopore pushed into the interior of the animal by the secondary invagination that forms the actinopharynx, and further drawn out into ribands by the downgrowths from the actinopharynx which attach themselves to the edges of the mesenteries and form the craspeda.

The Acontia.—I have been successful in obtaining good and truly transverse sections of these structures, and have to make the following remarks about them. They appear to me to be direct outgrowths of the telocraspedon (craspedion of Carlgren) of the first couple of metamesenteries, and I can find no trace of the ascending and descending limb round the edge of an attenuated outgrowth of the mesentery as described by Carlgren. Pl. 4, fig. 22, represents a highly magnified section through the middle of an acontium; Pl. 5, fig. 23, the origin of an acontium from the telocraspedon under less magnification. As Carlgren describes, the bulk of the acontium is made up of large goblet-shaped gland-cells, of which the contents stain greenish-yellow in picro-indigo-carmine, but intensely blue-black in hæmatoxylin, this colour-reaction indicating that they are mucus-secreting cells. Interspersed among them are a few goblet-cells with conspicuous eosinophilous granules. Nematocysts are scanty; those that are present are of the thick-walled variety and resemble those found in the cnido-glandular tracts; one of them is shown in Pl. 3, fig. 18A. The large curved sausage-shaped nematocysts so abundant in and characteristic of the endoderm of the sides of protomesenteries II and the fertile metamesenteries are never present in an acontium, but at the bases of these structures the mesentery, devoid of any craspedal thickening and with its edge simply covered with

unmodified endoderm cells, is continued for some little distance aborally, and here the large sausage-shaped nemato-cysts are abundant. In a prolonged search with an immersion lens I have failed to find any spirocysts in the acontia, though, as shown in Pl. 4, fig. 23, they are present in the telo-craspedon right up to the point of origin of the acontium. The presence of thick-walled nematocysts and the absence of the characteristic endodermal sausage-shaped nematocysts indicate that the acontium is, as Carlgren urges, an ecto-dermal outgrowth, and it more nearly resembles a cnido-glandular than a spirocyst-glandular modification of the craspedon. It is clearly mucus-secreting rather than urtica-tory in function. But as far as my own observations go, I cannot find in it any of the characters of a craspedoneme. Nevertheless, Carlgren, who was able to compare these structures in different species, is very possibly right in his contention that they are by origin craspedonemes, i. e. narrow riband-like outgrowths of the mesentery with ascending and descending limbs of the craspedon along their edges. In, this they differ from the acontia of Sargartiidæ and Phelliidæ, but the latter are not so very different in origin, for I think it must be conceded that they also are very narrow riband-like outgrowths of the mesenteries, but with a craspedal outgrowth along one edge only. Unquestionably, the so-called acontia of Cerianthids have arisen quite independently of the true acontia of Sagartiidæ and differ from the latter both in struc-ture and in function, but they are remarkably similar both in general appearance and in situation.

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